*Evolution of altruism*

# Altruism

**- behavior that benefits a receiver at a cost to the actor**

Examples:

- Honey bee sting
- Alarm calls
- Blood sharing by bats

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# Mutualism vs. altruism

Cooperation:

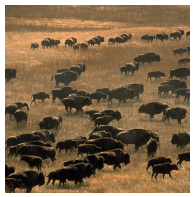
Displaying a behavior that benefits another individual. (If both benefit that's mutualism.)

Altrusim:

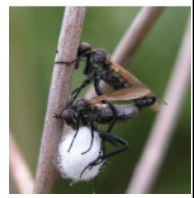
Displaying a behavior that benefits another individual at a cost to oneself.

*'Social behavior' is NOT cooperative behavior*

# Group living vs. cooperation



Sociality-no-cooperation and cooperation-no-sociality



I define 'sociality' as living with other individuals of the same species at least semi-permanently.

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# How can altruism evolve?

- If the recipient of the cooperative/altruistic act benefits, it is going to leave more offspring.
- The actor however is not going to leave more offspring, or even fewer offspring – **fewer altruists in the next generation**.

*If such behavior is heritable, and it goes on over many generations, it will ultimately die out.*

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# Selfish altruism?

If altruism was ultimately costly to reproduction, it would disappear in evolution.

- Altruism can occur at the level of individuals, but if we see it today, we have to assume that it benefits reproduction at some level in the long run (of genes, individual, or group).

*Evolution of altruism*

# Evolution of altruism

**Helping somebody at a cost to yourself - where are the hidden benefits?**

- Group selection – rare, only if long-term assortment maintained
- Kin-selection – yes, if helping relative
- Sexual selection – yes, if mating benefits
- Reciprocal altruism – yes, if reciprocation likely and enforced
- Status – yes, if indirect benefits

## Kin-selection

Helping relatives increases your 'inclusive fitness':

Inclusive fitness: your own offspring ('fitness') plus your genes reproduced in others.



## Kin-selection

Helping relatives increases your 'inclusive fitness' therefore means:

The more of your genes are in a relative, the more interest you have in helping them.



## Kin-selection

Helping relatives increases your 'inclusive fitness' therefore means:

The more of your genes are in a relative, the more interest you have in helping them.

**This is measured by r ('relatedness')**



## Relatedness 'r'

(also called coefficient of relationship)

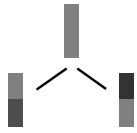
Usually defined as:

The average proportion of alleles of an individual A that are identical by descent to those in individual B.

Or, the probability that A and B carry the same allele, derived from the same ancestor, at a particular locus.



## Computing relatedness

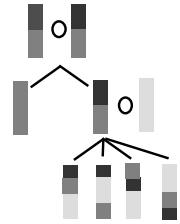


Relatedness: 0.5

If you have two children, on average one copy of each of your genes survives.



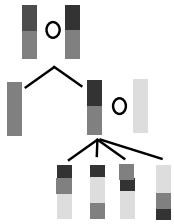
## Computing relatedness



If you have four nieces, on average one copy of each of your genes survives.

Relatedness: 0.25

# Kin-selection



This means, if you sacrifice yourself for four nieces, 'your genes' have lost nothing.



# Kin-selection

Hamilton's rule:

An individual can be altruistic if

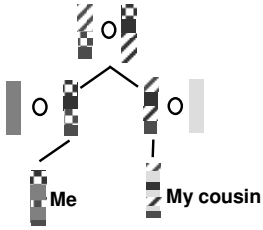
**c  b * r**

The cost should be smaller than the benefit multiplied by relatedness.

E.g. an individual may not reproduce in a given year (c=1) to help its sibling (r=0.5) if this helps the sibling raise at least two additional offspring (b=2).



# Computing relatedness

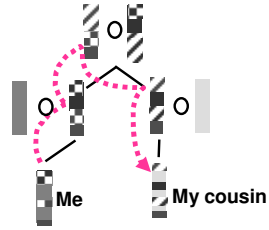



Values for a diploid, sexually reproducing individual:

| | |
|---|---|
| parent | 0.5 |
| sibling | 0.5 |
| uncle/aunt | 0.25 |
| cousin | 0.125 |
| grandparent | 0.25 |



# Computing relatedness

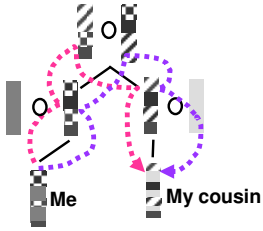



Trace back to common ancestor and then forward to target individual

0.5*0.5*0.5*0.5 = 0.0625



# Computing relatedness

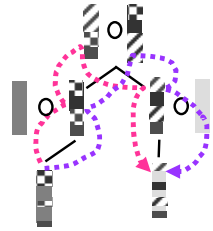



Trace back to common ancestor and then forward to target individual – then repeat with other common ancestors and add together.

0.0625 + 0.5*0.5*0.5*0.5 = 0.125



# Computing relatedness



Relatedness can thus be computed using a family tree ('pedigree').

# Relatedness 'r'

However, the definition that really reflects the 'r' in Hamilton's rule is:

**r is a measure stating how genetically similar the two individuals are relative to two random members of the population.**

This is on average the same as r calcutated by pedigree only in a large, randomly mating, outbred population. (Essentially, when inbreeding=0)



## Relatedness as measure of genetic similarity

Essentially 'r' is similar to measures of population structure (such as the inbreeding coefficient F).

*F = (expected – observed)/expected*

frequency of heterozygotes in a population

***r = (expected – observed)/expected***

**number of differing alleles between two individuals**



# Kin-selection

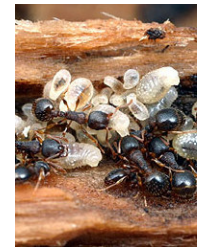
When it is demonstrated that individuals preferentially help kin rather than non-kin, this is taken as evidence for kin-selection.



# Kin-selection

Examples for kin-selection:

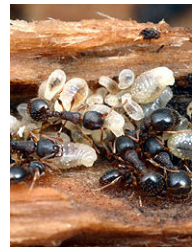
- social insects
- prairie dog alarm calls to offspring & other relatives
- generally parental care
- cells in our body





# Kin-recognition

Do individuals have to be able to recognize relatives for kin selection to work?





# Kin-recognition

**NO** – kin selection can operate, and cause the evolution of altruism, as long as altruists are more likely to help kin than non-kin - for whatever reason.

## Inclusive fitness theory vs. kin selection

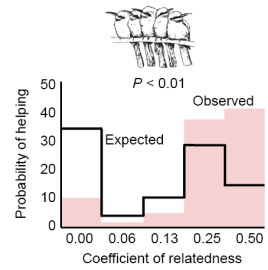
In fact, that's why some argue that it should be called 'inclusive fitness theory' rather than 'kin selection' –

**Altruism can evolve as long as altruists are more likely than chance to dispense help to other altruists.**

(see John's recent model on segregation)



## Kin-recognition






## Kin-recognition

- By smell (rodents, humans, insects)
- By song (some birds)
- By learning/familiarity (mice, humans)
- By visual similarity (chimpanzees, humans)

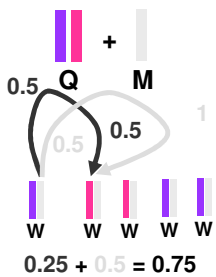


## The case of social insects

- Eusociality: some individuals sterile
- Evolved > 10 times in Hymenoptera (haplodiploid)
- All members of a colony are usually highly related



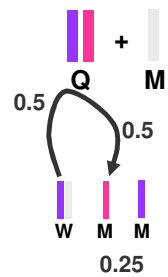
## Does haplodiploidy cause eusociality?




- In complete monogamy, **workers are more related to the queen's daughters (r=0.75) than to their own (r=0.5)**
- This would explain why so many Hymenoptera are eusocial
- and why workers are always females



## Does haplodiploidy cause eusociality?




- However, workers are only related to males by r=0.25 (less than to daughters) – thus average relatedness to reproductive offspring is still 0.5 (depending on sex ratio)
- Actual relatednesses measured in insect colonies are almost never 0.75 (multiple queens, polygamy)
- Recently more eusocial species without haplodiploidy have been discovered; and many haplodiploid species are not social

## Alternative hypotheses for the origin of eusociality

- Parental manipulation
- Predisposition to sociality because of high b/c ratio (underground nests, extended brood care)
- Group selection



## Wilson & Hölldobler 2005



## Wilson & Hölldobler 2005

- Superiority of colony life over solitary life (b may be much greater than c)
- Euociality arose among unrelated individuals first; then relatedness increased
- In many species nests are founded by unrelated individuals
- Real-existing relatedness low and counterproductive (?)
- Eusociality rare even in highly related groups



## Conclusions from the controversy

- Haplodiploidy is not crucial to evolution of eusociality
- Ecological factors (high b/c) explain most of the variation between species in sociality
- Controversy arises over the definition of 'r' – relatedness by pedigree or measure of genetic similarity?
- Complete worker sterility can only arise with positive r, whether by kinship or other segregation mechanisms
- However, many social insects do not actually have complete worker sterility



## Kin-selection

Hamilton' s rule: **c b * r**

- In a sense, kin selection is selection at the level of genes
- A behavior that is altruistic at the level of an individual could increase the representation of those genes in the next generation (increase inclusive fitness)
- Only works if altruism dispensed to genetically similar individuals



## Kin-selection

Hamilton equation: **c b * r**

- If studying the evolution of altruism, c and b are important!
- r should ideally be calculated as similarity relative to population variance
- If this is done, maybe it should better be called '**inclusive fitness theory**'

# Parental care – cooperation & conflict

- How is kin selection relevant to parental care?
- What predictions does kin selection make about parental care?



# Human altruism

- Is altruism in humans explained by kin selection?